

Habitat Differentiation of Ferns in a Lowland Tropical Rain Forest

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ABSTRACT.—Fern species and growth form diversity peak in tropical rainforests. In such forests, ferns often play important ecological roles. However the distribution and diversity patterns of different growth forms (i.e., epiphytic vs. terrestrial ferns) have not been broadly quantified. We compared the distribution and diversity patterns of epiphytic pteridophytes on the trunks of six individuals of the emergent canopy tree species *Hyeronima alchorneoides* (Euphorbiaceae) to those of terrestrial species at La Selva Biological Station in Heredia province, Costa Rica. A total of 21 species of epiphytic and 20 terrestrial ferns was recorded, with only one species found as an epiphyte and as a terrestrial species. Epiphytic species also exhibited increasing species diversity with increasing trunk height. Epiphytic species exhibited predictable patterns of distribution along the trunk and were easily grouped into high-trunk, low trunk, or bimodal categories. In terms of percent cover and number of species, simple-leaved ferns dominated the epiphytic growth form, 13 of 21 species, whereas ferns with compound or dissected leaves dominated the hemi-epiphytic and terrestrial floras with 20 of 20 species. These results indicate that there are significant functional differences in the ecology of epiphytic and terrestrial ferns and that reciprocal establishment is difficult and extremely rare.

KEY WORDS.—Pteridophyte, epiphyte, canopy, microclimate, gametophyte

Pteridophytes, especially the ferns, make up an important component of tropical and temperate floras and serve important functions in ecosystem processes in both the canopy (Hietz, 1997) and forest floor habitats (Hill and Silander, 2001). Epiphytic ferns make up an especially conspicuous component of tropical wet forest regions around the world. For example, in Costa Rica, 70% of the entire pteridoflora is epiphytic, while at La Selva Biological Station in northeastern Costa Rica epiphytic ferns comprise 42% of this lowland forest flora (Grayum and Churchill, 1987). Surprisingly, our understanding of the ecology of epiphytic taxa is especially limited.

Recent studies on the comparative biology of epiphytic and terrestrial fern species have revealed significant differences in the gametophyte ecology of these functional types (Watkins *et al.*, 2007a, b, c). Some epiphytic taxa have evolved fantastic degrees of desiccation tolerance in the gametophyte generation that likely contributes to establishment potential (Watkins *et al.*, 2007b) and ultimately controls species distributions. The gametophytes of epiphytic taxa also exhibit significant demographic differences from terrestrial species. Epiphytic gametophytes may live for years and perhaps decades and beyond, while their terrestrial counterparts have significantly reduced longevities (e.g. 1–2 months; Watkins *et al.*, 2007a). Such significant ecological differences do not disappear in the sporophyte generation and epiphytic taxa

exhibit divergent patterns of leaf-level nutrient and carbon relations relative to terrestrial taxa (Watkins *et al.*, 2007c).

What factors combine to influence the distribution of epiphytic and terrestrial species with such radical ecological differences? Most attempts to answer this question for epiphytes have focused on sporophyte ecology. Within canopy habitats, studies have demonstrated that water use efficiency and drought tolerance of sporophytes can affect epiphytic species distributions (Andrade and Nobel, 1997; Hietz and Briones, 1998). Epiphytic fern sporophytes also seem to be invested in biochemical (Hietz and Briones, 2001) and, to a more limited extent, morphological (Watkins *et al.*, 2006b) photoprotective measures which likely influence their distributions. Substrate preference also seems to play a significant role in structuring some species distributions (Moran *et al.*, 2003, Moran and Russell, 2004). Still others have attempted to quantify the effects of microclimate (Freiburg, 1998; Cardelús 2002; Cardelús and Chazdon, 2005), tree characteristics (Ter Steege and Cornelissen, 1989; Cardelús, 2002, 2007, Cardelús and Chazdon, 2005), and individual plant adaptations (Benzing, 1986, 1987) on overall epiphytic plant distributions.

In comparison to epiphytic species, our understanding of terrestrial species ecology is broader but remains limited for tropical species. Pioneering studies on the distributions of terrestrial ferns in the tropics have revealed the importance that edaphic specialization has on species distribution (Jones *et al.*, 2007, 2008; Tuomisto and Ruokolainen, 1994; Tuomisto and Dalberg, 1996; Tuomisto *et al.*, 1998; Tuomisto *et al.*, 2002). Sporophyte stress tolerance has also been demonstrated to influence the distribution of terrestrial tree fern species (Durand and Goldstein, 2001) and at the community level, both environmental and neighborhood effects have been shown to influence habitat specialization and act as an important determinant of the distribution of tree ferns (Jones *et al.*, 2007). While these studies have elucidated important aspects of fern ecology, few comparative studies on epiphytic and terrestrial species exist.

In a recent study comparing the distribution of epiphytic and terrestrial species along an elevational gradient, Watkins *et al.* (2006) found that out of 264 species only one grew as both a canopy epiphyte and a terrestrial species, and this from only a single site. A similar finding was reported by Kluge and Kessler (2006) along the same gradient in Costa Rica. Such a result is perhaps not surprising given the apparent ecological differences between these two groups. To understand better the patterns of fern habitat differentiation, we examined the vertical distribution of ferns on the trunk of an emergent canopy tree and compared this to species distribution in terrestrial plots. We asked the following questions: 1) How does overall species richness change and is there variation in the vertical distribution of epiphytic fern species along the trunks of an emergent tree species, 2) How does trunk fern richness and terrestrial fern richness compare and is there species overlap between habitats? 3) Are there differences in functional morphology between epiphytic and terrestrial species?

MATERIALS AND METHODS

Species composition and distribution.—This study was conducted at La Selva Biological Station in Heredia Province, Costa Rica. The site is a 1400 ha tropical wet forest with an average rainfall of 4000 mm per year (McDade *et al.*, 1994). The trunks of six *Hyeronima alchorneoides* Allemao (Euphorbiaceae) trees were sampled for ferns using single rope climbing techniques (Perry, 1978). *Hyeronima alchorneoides* was chosen as this evergreen species maintains relatively high epiphyte species richness and has a well studied canopy habitat (Cardelús, 2002, 2005; Cardelús and Chazdon, 2005). All trees sampled were greater than 1 m in diameter above the buttresses with an average diameter among trees of 1.5 m. A 26 m transect, from the forest floor to the main bifurcation was established along the trunk of each of six trees and broken into contiguous 2 m × by 2 m plots. We found that 26 m was an ideal length that put the upper bound of the transect just below the first trunk bifurcation of all trees sampled. This small size 2 m × 2 m plots established along the trunk allowed for a finer level analysis of richness and cover. The average trunk area sampled per tree was 122 m². Identity, abundance (estimated by measurements of percent cover) frond morphology, and life form (e.g., primarily epiphytic, primarily hemi-epiphytic, and primarily terrestrial) were documented for each fern species in each plot. While the actual number of individuals in a given plot may be a better measure of species richness, accurate counts of individuals from six trees was difficult. Species such as *Hymenophyllum brevifrons* Kunze (Hymenophyllaceae) form mats of potentially hundreds of individuals; thus, we utilized percent cover as a proxy for dominance and ignored the actual number of individuals. Percent cover was estimated by determination of the total area covered in each 2 m × 2 m plot by a given species. As leaves can overlap, it was possible to a plot to have a total percent cover of >100% when summed across species.

For comparison of epiphytic species with hemi-epiphytic and terrestrial species, a circular plot with a radius of 26 m (total sampled area of 2122 m²) was established terrestrially around the base of each sample tree. The 26 m radius plot was established to mimic the total tree height sampled. Each terrestrial plot completely encircled each sampled tree. The number of terrestrial individuals in these plots was often too low (4–5 individuals) to accurately allow for determination of percent cover; therefore, only presence/absence data was noted. Voucher specimens were collected from within each terrestrial plot and deposited in the National Herbarium of Costa Rica. For species identification we used the taxonomic concepts of Flora Mesoamericana (Moran *et al.*, 1995).

In addition to richness data, we quantified variation in leaf morphology among the different habitats sampled. Each species encountered was recorded as having compound or simple leaves. A chi square was run to determine if species from either habitat were associated with a given leaf morphology. We also evaluated specific leaf weight of species from three sections on the trunk. Data were collected from terrestrial plots, the buttress zone (0–2 m), and the

bifurcation zone (22–24 m). Due to limited time we choose these location subsets rather than sampling species along the entire trunk. The buttress zone and the bifurcation zone data also correspond to areas where we measured microclimate (see below).

Microclimate measurements.—Measurements of temperature and relative humidity were recorded on June 26, 2005. Three Hobo Pro Temperature/RH (Onset Corp., Bourne, ME, USA) data loggers were placed at three different locations on a single tree. One sensor was placed at 1.5 m above the forest floor to measure microclimate of the buttress zone, another sensor was suspended at 11 m above the forest floor to measure the mid-bole zone, and a final sensor at 23 m above the forest floor to represent the highest level or bifurcation zone. Temperature and humidity were recorded every 5 min for 12 hours. Water potential of the air was calculated using the formula: $\Psi = RT \ln e/e^0$, where R is the gas constant, T is the absolute temperature and e/e^0 is relative humidity expressed as a fraction (i.e. 50% r.h. = 0.5). This value was divided by the partial molal volume of water to convert to pressure units.

Light levels were measured with a Licor quantum sensor (Li-190, Lincoln, NE, USA) connected to a Licor data logger (Li-1400, Lincoln, NE, USA) at the same levels as temperature and humidity. Measurements were taken on June 27, 2005 and percent light transmittance was calculated by comparing sensor data to a control sensor measuring at the same time in an open field.

RESULTS

Species composition and distribution.—A total of 40 fern species was found: 21 epiphytic species (plus gametophytes of Vittariaceae), 15 terrestrial species and 4 hemi-epiphytic species (Table 1). *Olfersia cervina* (Dryopteridaceae), was the only species found in both habitats (Table 1). The average number of epiphytic species found per tree was 11 (+/–2 species) with the sporophytes of *Vittaria stipitata* Kunze (Vittariaceae), *Elaphoglossum herminieri* (Bory & Fée) T.Moore (Elaphoglossaceae), *Oleandra articulata* (Sw.) C.Presl (Dryopteridaceae), and Vittariaceae gametophytes occurring on all individual trees (Table 1). Examination of presence/absence data suggests that terrestrial species are less abundant relative to the epiphytic species (Fig. 1). In addition, no single terrestrial species was represented in all 6 terrestrial plots. Only a single hemi-epiphytic species, *Polybotrya osmundacea* Humb. & Bonpl. ex Willd., was found in all six terrestrial transects.

Even though a significantly lower total trunk area was surveyed in the epiphytic when compared to terrestrial habitats, we encountered a higher diversity of epiphytic relative to terrestrial and hemi-epiphytic species (Table 1, Fig. 1). The number of epiphytic species remained relatively constant along the trunk up to 16 m, when diversity quickly increased (Fig. 1). Abundance (% cover) of epiphytes along the trunk did not follow this trend, but showed a strongly bimodal distribution (Fig. 2).

Microclimatic variation and extremes were differentially distributed over the trunk (Fig. 3). The buttress zone was consistently darker and exhibited

TABLE 1. Trunk and terrestrial plots where epiphytic, terrestrial, and hemiepiphytic fern species were collected. Shaded squares represent presence of a given species in a given plot. Circular terrestrial plots with a radius of 24 m were established at the base of each sampled tree. Hemiepiphytic species were all recorded from these terrestrial plots. Data from this study were gathered from La Selva Biological Station in Costa Rica.

Epiphytic Species	Plot Height on Tree Trunk (m)											
	0-2	2-4	4-6	6-8	8-10	10-12	12-14	14-16	16-18	18-20	20-22	22-24
<i>Coelidium serrulatum</i> (Sw.) Bishop												x
<i>Grammatid</i> sp. 1												x
<i>Microgramma lycopodioides</i> (L.) Copel.												x
<i>Phlebodium pseudoaureum</i> (Cav.) Lellinger												
<i>Elaphoglossum</i> sp. 2												
<i>Microgramma reptans</i> (Cav.) A.R. Sm.									x			
<i>Elaphoglossum</i> sp. 1									x			
<i>Polypodium triseriale</i> Sw.								x				x
<i>Hymenophyllum brevifrons</i> Kunze						x		x	x			x
<i>Elaphoglossum herminieri</i> (Bory ex Fei) T. Moor			x	x	x	x	x	x	x			x
<i>Nephrolepis rivularis</i> (Vahl) Mett. ex Krug.			x	x	x	x			x			x
<i>Oleandra articulata</i> (Sw.) Presl			x	x	x	x	x	x	x			x
<i>Vittaria stipitata</i> Kunze			x	x			x	x	x			x
<i>Hecistopteris pumila</i> (Spreng.) J. Sm.		x					x	x	x			x
<i>Asplenium serra</i> Langds. & Fischer	x	x			x			x	x			x
<i>Hymenophyllum</i> sp. 1	x	x	x	x	x	x		x	x			x
<i>Elaphoglossum latifolium</i> (Sw.) J. Sm.	x	x	x	x	x		x	x	x			x
Vittariaceae Gametophytes							x	x	x			x
<i>Trichomanes godmanii</i> Hook.	x	x	x	x								
<i>Trichomanes ekmanii</i> Wess. Boer	x	x	x									
<i>Olfersia cervina</i> (L.) Kunze	x											

Terrestrial Species	Plot Number					
	1	2	3	4	5	6
<i>Dennstaedtia dissecta</i> (Sw.) T. Moore			x		x	x
<i>Adiantum obliquum</i> Willd.	x	x				x
<i>Alsophila cuspidata</i> (Kunze) D.S. Conant	x	x				
<i>Cyathea multiflora</i> J. Sm.					x	x
<i>Danaea wendlandii</i> Reichenb. F.		x				x
<i>Adiantum latifolium</i> Lam.				x		
<i>Blechnum occidentale</i> L.						x
<i>Diplazium macrophyllum</i> Desv.						x
<i>Pteris podophylla</i> Sw.						x
<i>Saccoloma inaequale</i> (Kunze) Mett.	x					
<i>Salpichlaena volubilis</i> (Kaulf.) J. Sm.		x				
<i>Tectaria draconifolia</i> (D.C. Eaton) Copel.				x		
<i>Tectaria incisa</i> Cav.			x			
<i>Thelypteris curta</i> (H. Christ) C.F. Reed						x
<i>Thelypteris nicaraguensis</i> (E. Fourn.) C.V. Morton		x				

Hemiepiphytic Species	Plot Number					
	1	2	3	4	5	6
<i>Polybotrya osmundacea</i> Humb. & Bonpl. ex Willd.	x	x	x	x	x	x
<i>Olfersia cervina</i> (L.) Kunze				x		x
<i>Lomariopsis vestita</i> E. Fourn.	x	x				
<i>Polybotrya caudata</i> Kunze	x					

significantly wetter air and less variation than the mid-trunk or bifurcation zone. Variation increased along the trunk with the most extreme and variable microclimate occurring in the bifurcation zone (Fig. 2).

There were also several species specific distribution patterns. For example, *Elaphoglossum sp.1* is a high light, high canopy species, whereas its congener *Elaphoglossum latifolium* (Sw.) J.Sm. seems to tolerate more variable microhabitats often occurring in the dark, wet buttress zone (Fig. 4). A similar pattern exists between *Hymenophyllum brevifrons*, a high canopy species, and the related *H. hirsutum* (L.) Sw. which follows a bimodal pattern similar to *E. latifolium*. In contrast, a pair of filmy ferns, *Trichomanes godmanii* Hook. ex Baker and *T. ekmanii* Wess.Boer are present at high densities on the low trunk and buttresses but neither occur in high canopy locations.

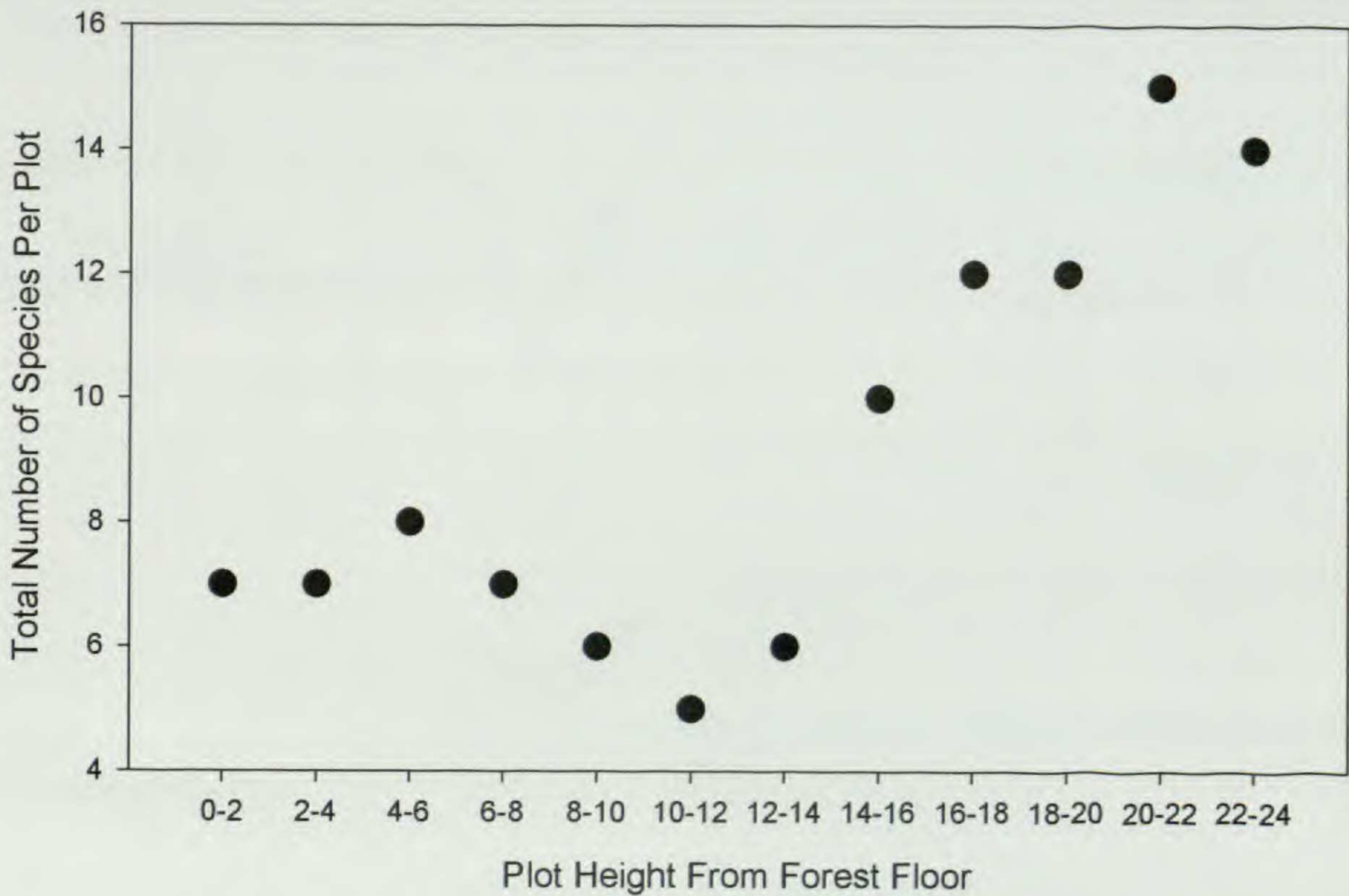


FIG. 1. Epiphytic, terrestrial, and hemiepiphytic fern species area curve sampled at La Selva Biological Station, Costa Rica. Epiphytic species were recorded on the trunks of six emergent canopy trees (*Hieronima alchorneoides*) whereas terrestrial and hemiepiphytic species were collected in ground transects under each sampled tree.

Another intriguing distribution pattern unfolds when members of the Vittariaceae are examined. Due to their unique gemmae production (asexual propagules), we were able to identify the gametophytes of this family (Farrar, 1974). The gametophytes exhibit an interesting bimodal distribution occurring at both the buttress and the crown, while sporophytes of *Vittaria* were only encountered on high trunks (Fig. 5).

Fronde Morphology.—When frond morphology was examined in epiphytic, terrestrial and hemi-epiphytic species, epiphytic ferns had significantly more species with simple leaves than terrestrial and hemi-epiphytic species ($\chi^2 = 18.13$; $p = 0.0001$) Thirteen of the 21 epiphytic species had simple leaves and there were no terrestrial or hemi-epiphytic species exhibiting this leaf morphology. Specific leaf weight also increased from terrestrial to bifurcation zone species (Fig. 6)

DISCUSSION

Species distributions.—In the first part of this study, our goal was to describe and compare the abundance (in terms of percent cover) and distribution patterns of epiphytic ferns in canopy habitats to determine if there is predictable vertical distribution of epiphytic fern species along the trunks of an emergent tree species. When the total number of species per plot was

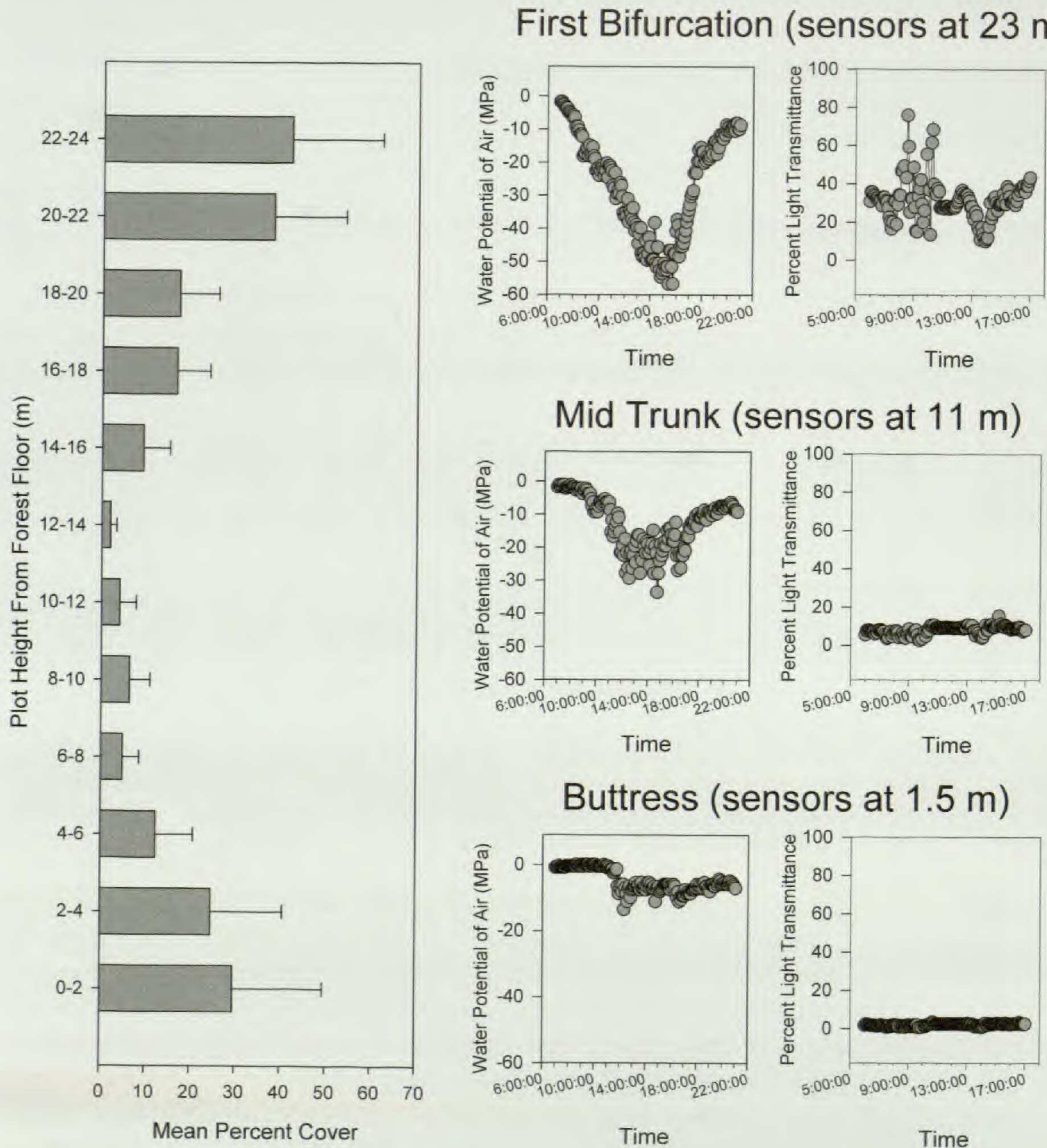


FIG. 2. The bimodal relationship of mean percent cover of all epiphytic fern species along sampled tree trunks. Humidity and light sensors were placed at three separate locations along the trunk: 1.5 m, 11 m, and 23 m. Microclimatic variables and light were measured at 5 min intervals at these locations.

examined, there was a predictable pattern of increasing species diversity with plot/tree height above 12 m (Fig. 3). The lower buttress zone (0–2 m) of any given tree was less diverse than the top bifurcation zone (22–24 m, Fig. 3). While diversity increased, percent cover exhibited a highly bimodal distribution (Fig. 2). Thus, while the number species increase with plot height, the total percent cover was similar between buttress and bifurcation zones. The buttress zone is homogeneously dark and wet whereas the mid- and upper-trunk are brighter and drier and exhibit greater environmental

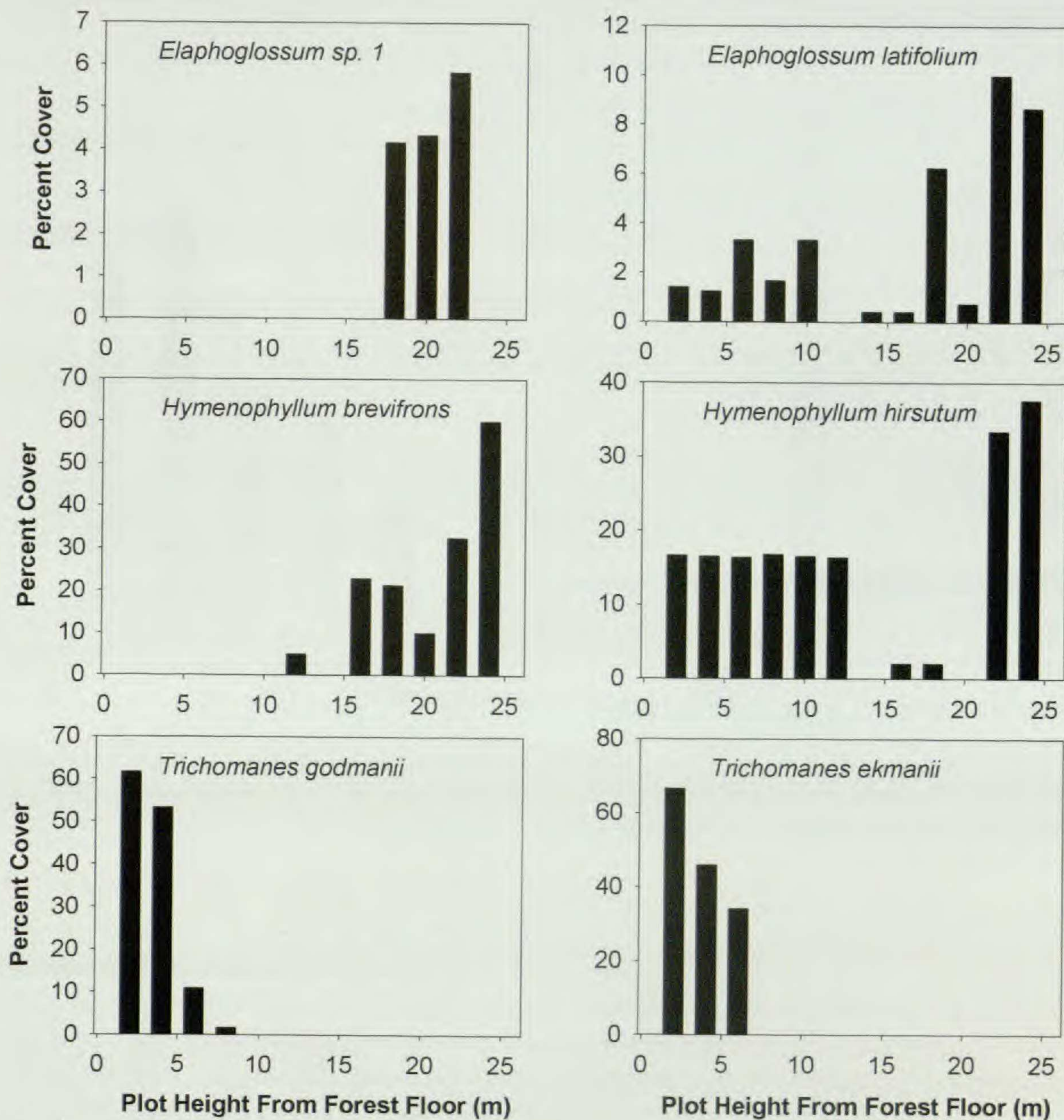


FIG. 3. The relationship of trunk height above ground on *Hyeronima alchorneoides* with the richness of epiphytic fern species. Highest richness was consistently within 2–3 m of the first branching of the trunk.

heterogeneity (Fig 2). These factors likely contribute to differences in diversity and abundance along the trunk. Indeed, whereas edaphic characters have been shown to influence terrestrial species diversity, light and water likely play an important role in shaping epiphytic species distribution (Hietz and Briones, 1998). Our data suggests that microenvironmental heterogeneity, rather than absolute values, is particularly important for epiphytic ferns.

Along with the zone specific microclimatic variation, we also found broad species specific patterns of distribution. The filmy ferns *Trichomanes ekmanii* and *T. godmanii*, dominated the dark buttress zone. The group, “filmy ferns,” get their name from fronds that lack stomata, are one cell layer thick, and thus

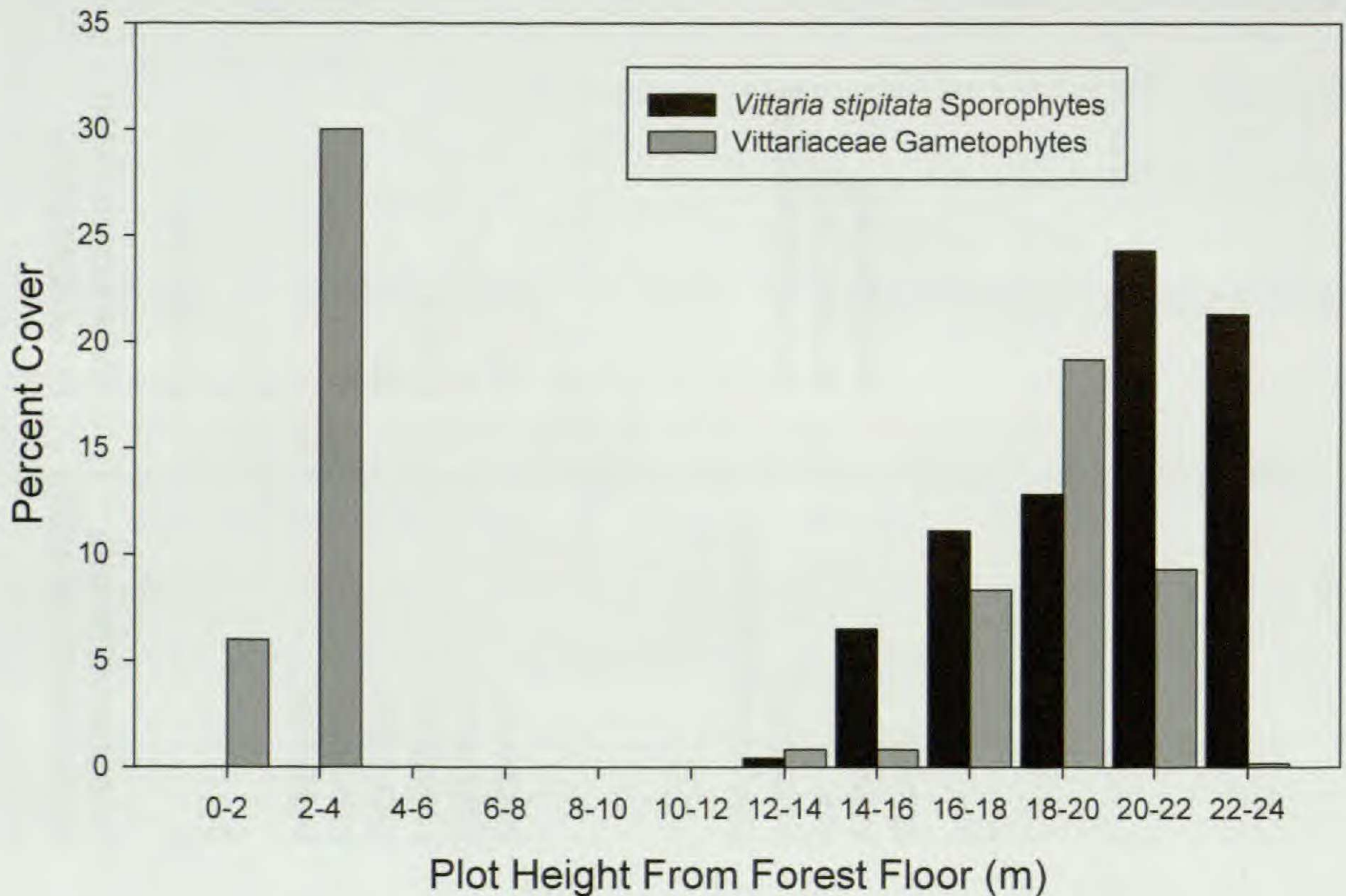


FIG. 4. Examples of a subset of epiphytic species distribution along the trunks of *Hyeronima alchorneoides*. Most species fell out into primarily buttress species or bifurcation species with few occurring across the trunk.

prone to desiccation. It is not uncommon to find large scale mortality of these two species following tree falls that expose them to brighter drier environments (pers. obs). *Hymenophyllum brevifrons* is similar in size to *T. ekmanii* and *T. godmanii* yet is completely absent from the dark buttress areas and quite abundant in high trunk habitats. *Hymenophyllum hirsutum* had a much broader range, occurring in most plots along the trunk (Fig. 4). The upper trunk had both a high percent cover and high species diversity which may reflect a more heterogeneous microenvironment to which different ferns are adapted. This variation may be important in maintaining high levels of fern diversity in tropical forests, especially on small local scales employed in this study.

An additional pattern to emerge from this study is the differential distribution of the gametophytes and sporophytes of the Vittariaceae. While the area remains poorly studied, it is thought that gametophytes may exhibit broader ecological distributions than their sporophyte counterparts (Sato and Sakai, 1980; Sato and Sakai, 1981; Peck *et al.*, 1990). Vittarioid gametophytes are easily identifiable given their unusual morphology and gemmae production. We observed that Vittarioid gametophytes exhibited a distinctly bimodal distribution relative to sporophytes which were confined to plots higher along the trunk (Fig. 5). There was not a single Vittarioid sporophyte below 4 m on any of the trees sampled. We encountered hundreds of gametophytes from potentially several different non-Vittarioid species which suggests that the

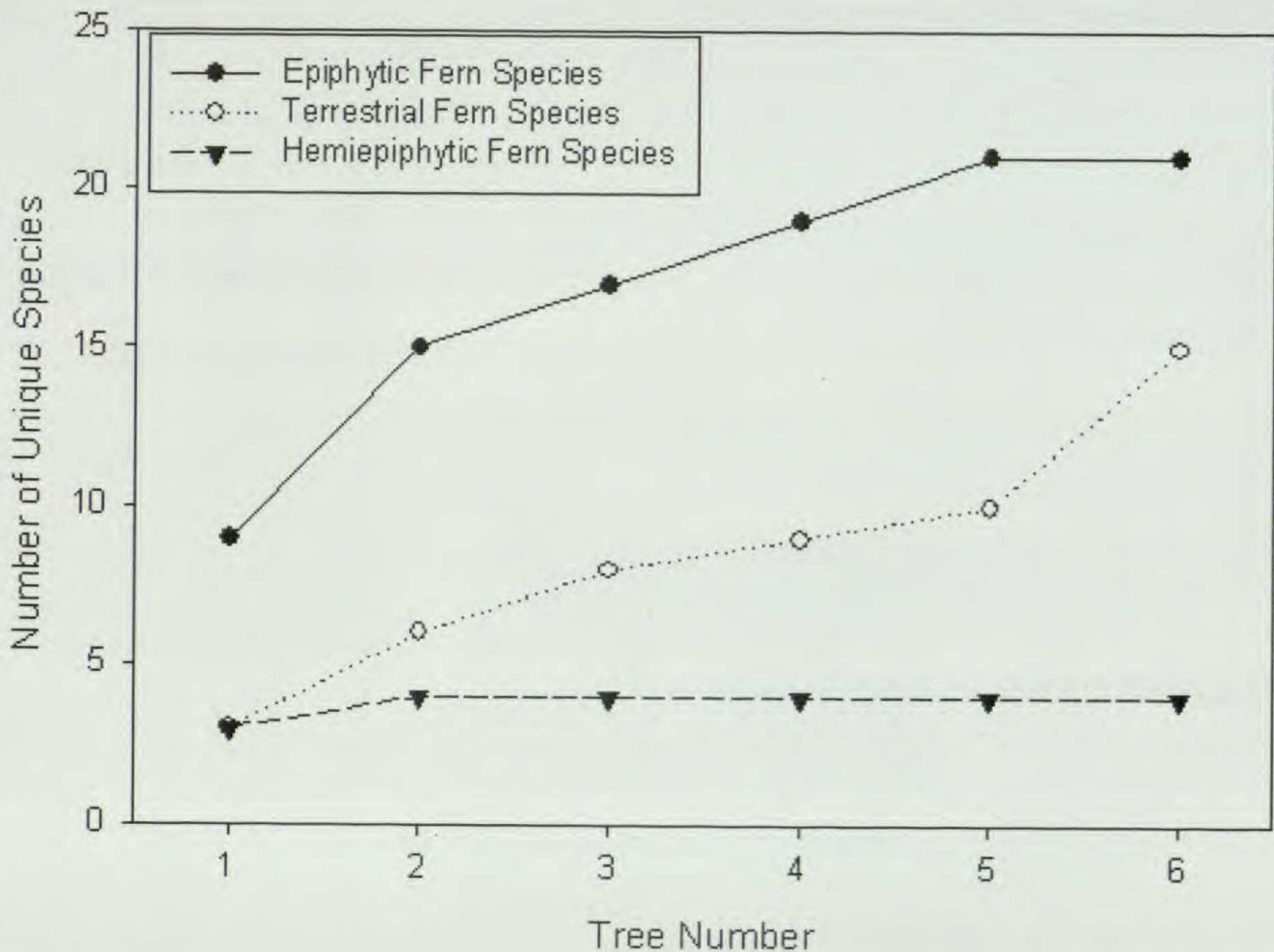


FIG. 5. Distribution of sporophytes and gametophytes of the Vittariaceae. Sporophytes are only found on the upper portions of the trunk, whereas gametophytes were found in both the upper portions and lower portions of the trunk.

gametophytes of other species may exhibit similar patterns of distribution. Gametophytes may be more highly adapted to growth in dark environments as the carbon budget of an individual, and thus growth rates, are small compared to the needs of the sporophyte (Farrar, 1998). Whereas gametophytes can establish in a broader range of environments, sporophytes may be more restricted to more stable niches. Greater ecological plasticity in the gametophyte generation may be important in "habitat exploration" for species as it is the first living stage to encounter new environments. Data from temperate species has shown that gametophyte plasticity is important to establishment and sporophyte distributions (Greer *et al.*, 1997).

Species diversity.—The second part of this study examined how trunk fern diversity and terrestrial fern diversity compare and asked if there is species overlap between habitats. The area sampled on all six trees was less than the area sampled in the first terrestrial plot, yet the number of epiphytic species is much higher than terrestrial species (Fig. 1). As with any study on tropical species diversity, our species area curve indicates that we under-sampled terrestrial species. We ceased to discover any additional epiphytic species, yet we know from an earlier floristic survey of La Selva (Grayum and Churchill, 1987) that this too represents an underestimation of epiphytic and hemi-epiphytic species.

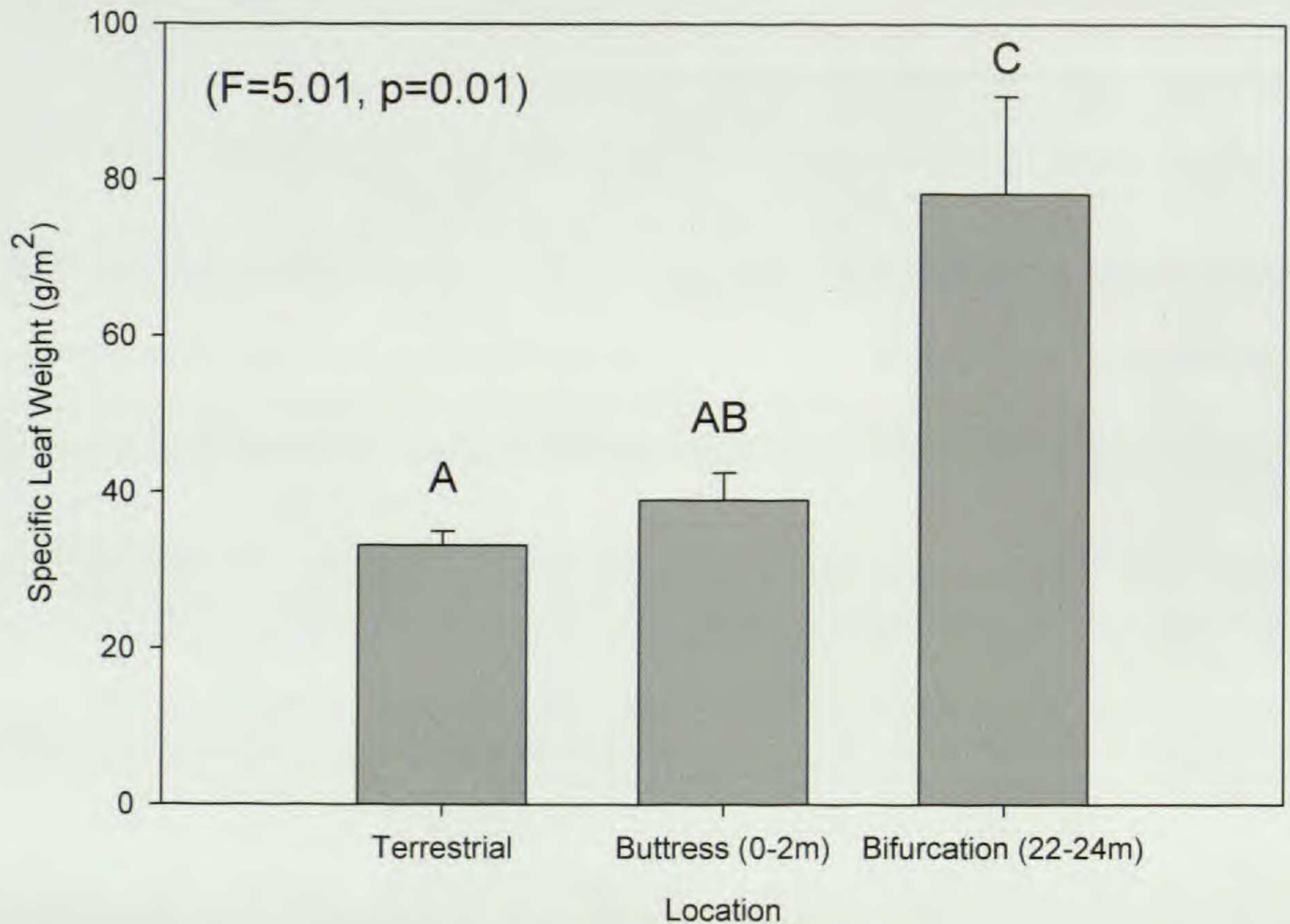


FIG. 6. Specific leaf weight of terrestrial, buttress epiphytes, and bifurcation epiphytes growing on *Hyeronima alchorneoides* at La Selva Biological Station, Costa Rica.

Nevertheless, in this study, epiphytic species were more diverse than terrestrial and hemi-epiphytic species. While it has been difficult to show that host specificity influences epiphyte composition (Zotz and Vollrath, 2003) it is known that certain tree species harbor greater diversity and numbers of epiphytes (Cardelús, 2002). The tree chosen for this study has a diverse and abundant epiphyte flora relative to other emergent tree species in La Selva.

The epiphytic fern flora of *Hyeronima alchorneoides* makes for interesting comparisons with the terrestrial fern flora as the species grows on both alluvial bottoms and upland terraces. We were thus able to sample a diversity of soil types and found that alluvial bottoms were areas of particularly high terrestrial fern diversity. For example, the final terrestrial transect sampled happened to occur along a small stream on one of the alluvial bottoms at La Selva. The number of terrestrial species in this particular plot was almost double that of the most diverse terrestrial plot in the sample. While other factors may be involved, this observation further supports the importance of edaphic factors to patterns of terrestrial fern distribution (Tuomisto and Ruokolainen, 1994; Tuomisto and Poulsen, 1996; Tuomisto *et al.*, 1998).

When we examined the species overlap between habitats, we found that *Olfersia cervina* was the only species that was found growing in epiphytic and terrestrial habitats. This species has been described as a low climber (Moran, 1995) and as a hemi-epiphyte which could exclude it from both the epiphytic

and terrestrial groupings. The species was only observed in pockets of deep soil that form on buttresses and never above 2 m from the forest floor. This is an unusual species in that it is most frequently encountered growing on large fallen trees in advanced stages of decay (pers. obs). *Hyeronima* often forms buttresses that can collect large amounts of detritus and thus provides an important habitat for *Olfersia*. Perhaps of greater interest is that there was not a single species that grew on terrestrial soil and on the upper trunk further corroborating the reports by Watkins *et al.* (2006). One question that has often plagued pteridologists is how the evolution of epiphytism actually came about. In spite of the fern's dispersal syndrome, such intensive local sampling effort combined with regional studies (Watkins *et al.*, 2006) suggest that reciprocal establishment of epiphytic and terrestrial species is rare. In the ferns, epiphytism likely arose through some intermediate form, most likely passing through some hemi-epiphytic form before radiation into a completely epiphytic condition.

Leaf morphology.—There are striking differences in leaf morphology between the epiphytic and terrestrial species studied here. The majority of epiphytic species (13 of 21) have simple leaves whereas terrestrial and hemi-epiphytic species have compound morphologies. Interestingly, of the epiphytic species with compound leaves, only two species in the Hymenophyllaceae had leaves that were more than once pinnate. In an opposite pattern, 11 of the 15 terrestrial species exhibited leaves that were more than once divided; the other four species had once pinnate leaves. These patterns are repeated throughout the Costa Rican pteridoflora (pers. obs) and this convergence of leaf form in the canopy, in several divergent lineages, suggests that these traits are adaptive and are under direct selective pressure. Epiphytic species from the bifurcation zone also had significantly increased specific leaf weight compared to terrestrial and buttress epiphytes. Canopy habitats tend to be hotter, drier (Fig. 2), and experience more wind than terrestrial habitats in most tropical forests. Thus, it is likely that the combination of both energy and mechanical aspects have influenced the evolution of leaf morphology and leaf thickness in epiphytes.

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